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DISTRIBUTION AND ECOLOGY OF MYSIDS IN CAPE COD BAY, MASSACHUSETTS

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ABSTRACT

Seven species of mysids (*Neomysis americana, Erythrops erythropthalma, Mysis stenolepis, Mysis mixta, Heteromysis formosa, Praunus flexuosus*, and *Meterythrops robusta*) were collected from Cape Cod Bay, Massachusetts. The general ecology of the first four species is described in terms of several classificatory schemes proposed for worldwide mysid distributions.

Organismal relationships to geographic, seasonal, bathymetric, bottom water temperature, and sediment characteristics are examined. Four species occurred year-round with the following seasonal peaks in abundance: *N. americana* (February, April, December), *E. erythropthalma* (January, March, December), *M. mixta* (March and July), *M. stenolepis* (January and August). Based on bathymetric and sedimentary relationships the species tend to occur in pairs. *Neomysis americana* and *M. stenolepis* were primarily collected in shallow water (10–29 m) and from sand and clayey-silt. *Erythrops erythropthalma* and *M. mixta* occurred in deeper water (20–39 m) and on clayey-silt and silt. In addition to seasonal effects, evidence indicates that interactions among depth, bottom water temperature, and sediment type strongly influenced the spatial zonation of Cape Cod mysids. The distribution and ecology of the four mysids generally conformed to worldwide classification schemes.

INTRODUCTION

The Cape Cod Bay, Massachusetts biotic census was conducted to provide data on species composition, abundance, diversity, and trophic groupings of marine benthic organisms in regard to biotic and abiotic factors, and to provide a base for systematic and ecologic investigations of the Cape Cod Bay ecosystem and for assessment of change brought about by human activities (Carriker, 1972). The present account focuses on the mysidaceans from the biotic census.

Since mysidaceans form a conspicuous component of macrozooplankton in freshwater and oceanic environments and can form an important resource in food web dynamics, they have been extensively studied (Gordan, 1957). Research along the northeast coast of North America reflects this worldwide interest (Verrill *et al.*, 1873; Rathbun, 1905; Bigelow and Sears, 1939; Bousfield, 1956, 1961; Brunel, 1960; Wigley, 1963; Haefner, 1968). Although mysids are commonly considered to be planktonic, studies with a variety of bottom collectors have shown that some species are benthic or spend some portion of their life on the bottom (Clutter, 1967; Murano, 1970a, b). Based on 3×10^6 specimens collected from 1953 to 1969 from the continental shelf and slope between Canada and southern Florida, bathymetry, bottom

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sediment, and generation type were recognized as important features influencing mysid distribution (Wigley and Burns, 1971). In a comprehensive review Muachline (1980) proposed several classifications to describe worldwide mysid distributions based on these features. This research examines whether mysidaceans collected by the Cape Cod Bay biotic census were responding to the same features underlying Mauchline's (1980) classifications for worldwide distributions.

Cape Cod Bay is described elsewhere (Young and Rhoads, 1971). It encompasses 1600 km^2, is circular, and opens northward to Massachusetts Bay (Figure 1). Mean tidal range at Plymouth, Massachusetts is 2.9 m. Average annual extremes of surface temperature (−0.1 and 19.9°C) and salinity (31.0 and 33.2‰) are similar to bottom temperature (−0.1 and 17.7°C) and bottom salinity (31.2 and 32.3‰). Bottom temperatures ranged from −1.5 to 23.5°C. Highest and lowest values of both hydrographic features are normally associated with surface waters. A summer thermocline appears in April and disappears in October. Reverse thermoclines may occur at 15 to 25 m during mid-winter when bottom water may be 1 to 2.5°C warmer than surface water. Sediments consist of a mixture of clayey-silt, silt, sand, and gravel. Sand and silt each comprise approximately 40–45% of the bay sediments, and gravel comprises the smallest component of sediment (Young and Rhoads, 1971).

Materials and Methods

The methods used to collect and process the samples are described in detail by Young *et al.* (1971). Since the goals of the study were to maximize the number of

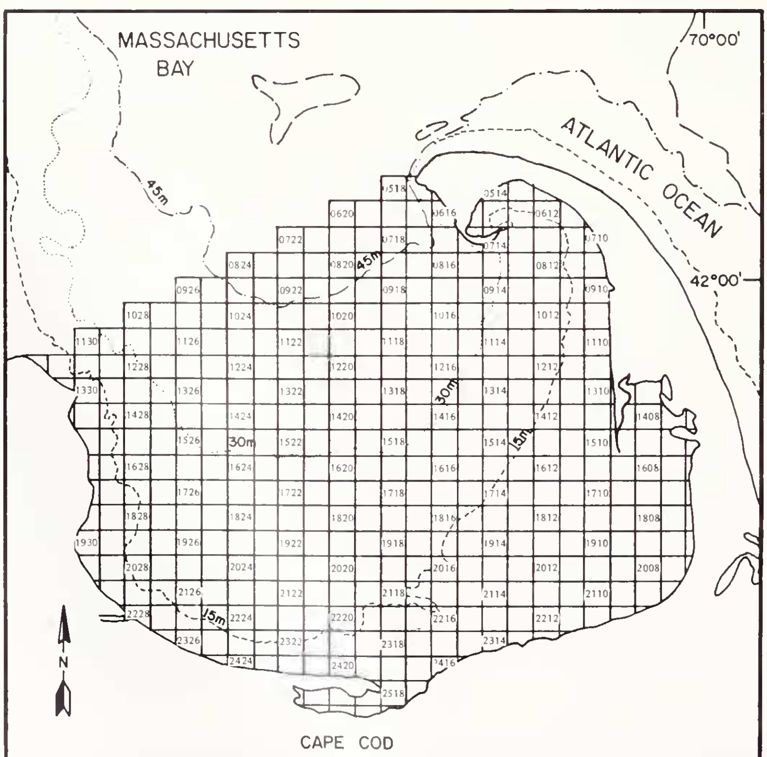

FIGURE 1. Location of station quadrats, Cape Cod Bay, Massachusetts.

different locations sampled, no repetitive sampling over time was conducted. Cape Cod Bay was divided into one square mile quadrats (Figure 1). Sampling was conducted from 1966 to 1969, yielding samples from each month of the year. Although the sampling effort was evenly distributed over the bay, based on sediment distribution approximately 36.6 percent of the samples were taken from mud >4ϕ (where ϕ = median sediment particle size; 0.062 mm), 42.5 percent from very fine to coarse sand 1–4ϕ (0.062–0.50 mm), and 20.9 percent from coarse sand to gravel. Thus there is bias towards samples from coarser grained sediment. It should be emphasized that sampling was not synoptic and that seasonal patterns are based on a composite of samples collected over several years. Quadrats were sampled randomly over sediment type and depth range.

Quantitative samples were taken from the center and four corners of each complete quadrat by a Smith-McIntyre grab (0.1 m^2). Dredge hauls were obtained from three of the corners by towing to the center of each quadrat. The dredge types included an epibenthic sled, a modified commercial clam dredge, and a naturalist dredge.

Quantitative samples were washed immediately by elutriation with sea water into 1.0 and 0.5 mm screens, and dredge hauls were washed through the former. The washed residue on each screen was placed for 5–10 minutes in a 0.15% solution of propylene phenoxytol in sea water. Specimens were preserved in a 10% solution of formalin in sea water for 48–72 hours, rinsed with tap water for several minutes, and transferred to 85% ethyl alcohol for final storage. Preserved samples of mysids were sorted according to species, sex, and life stage and counted under microscopes.

Four hundred and sixty grab samples and 260 dredge hauls were collected. At the center of each quadrat, surface and bottom temperature and salinity were measured. Sediment cores for analysis of particle size were taken from each Smith-McIntyre sample and frozen until analyzed. A total of 320 sediment samples were analyzed. Textural analysis was done by dry sieving the sand fractions through an Udden-Wentworth sieve series on a RoTap shaker following initial dispersion with sodium metaphosphate. The silt and clay fractions were determined by pipette analysis. For purposes of this presentation gravel is defined as $> -1.0\phi$, sand -1.0 to 4.0ϕ, silt 4.0 to 5.0ϕ, and clayey-silt >5.0ϕ.

The number, sex, and life stage (adult, immature, ovigerous, larvigerous) of individuals per each species of mysid were tabulated. The density (grab), relative abundance (dredge), and frequency (percent of occurrence) in grab and dredge samples were compared to environmental factors with correlation coefficients (R). Density was transformed by $\log_e (N + 1)$ prior to correlation. Analysis of covariance was performed on monthly density counts using biomedical computer programs from the University of California, Los Angeles. The program produced an analysis of variance for adjusted group means and a *t*-test matrix for adjusted group means. This procedure was used because of unequal data sets and because it tests whether the means of the dependent variable are significantly different among groups and whether the difference is due to differences in the independent variable among the groups (Snedecor and Cochran, 1967; Sokal and Rohlf, 1969).

Results

General occurrence

Neomysis americana (Smith) was collected most frequently followed in descending frequency by *Erythrops erythropthalma* (Goes), *Mysis mixta* Lillgeborg, and *Mysis stenolepis* Smith. *Neomysis americana* occurred throughout the bay except the north central portion whereas *E. erythropthalma* and *M. mixta* occurred everywhere except the southern and southeastern portion. *Mysis stenolepis* occurred mainly in the southern half of the bay with a few occurrences in the northern half. Several specimens of *Heteromysis formosa* (Smith) and *Praunus flexuosus* (Müller) and a damaged specimen questionably assigned to *Meterythrops robusta* (Smith) were also collected.

Seasonal distribution

Neomysis americana was collected every month with abundance peaks in February, April, and December (Table I). Based on Analysis of Variance (ANOVA, F = 2.48, D.F. 66,360) the effect of month of collection was statistically significant ($\alpha = 0.01$). Examination of the t-test matrix for adjusted group means of grab samples indicated that catches from February, April, and December were significantly different ($\alpha = 0.05$) from those in other months. Patterns based on dredge data showed high relative abundance during the same three months.

The overall sex ratio of adults was 0.51 males to 1 female (grab) and 0.82 males to 1 female (dredge). Dredge hauls yielded ovigerous stages in October and larvigerous stages from April through October.

Erythrops erythropthalma was collected every month, and number collected peaked in March and December (Table I). Based on ANOVA (F = 1.6, D.F. 66, 360), the effect of month was statistically significant ($\alpha = 0.01$). The t-test matrix for grab data indicated that January and December were significantly different ($\alpha = 0.05$). Trends depicted by dredge data indicated relatively large numbers January through April (Table I).

Density of *E. erythropthalma* decreased throughout spring and summer (May–August). The overall sex ratio of adults was 0.32 males to 1 female (grab) and 0.53 males to 1 female (dredge). Dominance in sex ratio of *E. erythropthalma* changed more frequently throughout the year than did that of *N. americana*. June and November were the only months when immature forms were not collected by dredge. Dredge collections produced ovigerous stages in May and July (Table I). Larvigerous stages were collected in January, May–September, and December.

Mysis mixta was collected every month but October (Table I). Based on ANOVA (F = 2.7, D.F. 66,360), the effect of month of sampling was significant ($\alpha = 0.01$). the t-test matrix for grab data indicated that the majority of monthly samples were significantly different ($\alpha = 0.05$) from one another. Dredge data indicated a peak in March followed by a rapid decline and gradual increase through July (Table I). Immature forms occurred from April to July. Ovigerous forms were collected in January and December, and larvigerous stages were taken from January to April. The sex ratio of adults was 0.02 males to 1 female (grab) and 0.07 males to 1 female (dredge).

Results for *M. stenolepis* are primarily based on dredge data as less than 2% were collected quantitatively (Table I). *M. stenolepis* was collected every month, with peak abundances in January and August. Ovigerous forms were only collected in January, whereas larvigerous forms were collected in January, March, and April. The sex ratio of adults was 0.1 males to 1 female.

Relationship to bathymetry

Most *N. americana* in Cape Cod Bay were collected in shallow to intermediate depths (Table II). There was a rapid decline in number caught at depths greater than 40 m. The highest density occurred at 30–39 m and the highest relative abundance

TABLE I

Monthly distribution of Neomysis americana, Erythrops erythropthalma, Mysis mixta *and* Mysis stenolepis *by sex and stage in Cape Cod Bay.*

	Grab (No./m²)					Dredge (No./haul)						Grand total	Grab (No./m²)					Dredge (No./haul)						Grand total
	M	F	Imm	Lar	Total	M	F	Imm	Ovig	Lar	Total		M	F	Imm	Lar	Total	M	F	Imm	Ovig	Lar	Total	
	Neomysis americana												*Erythrops erythropthalma*											
Jan	5	33	5	0	43	39	131	34	0	0	204	247	8	22	14	0	44	41	90	23	0	2	156	200
Feb	122	90	20	0	232	168	72	15	0	0	255	487	13	9	2	0	24	52	71	17	0	0	140	164
Mar	4	13	2	0	19	32	63	8	0	0	103	122	11	27	16	0	54	182	317	116	0	0	615	669
Apr	38	120	8	0	166	380	142	61	0	2	585	751	2	23	8	0	33	71	49	16	0	0	136	169
May	2	6	0	1	9	76	86	7	0	24	193	202	1	6	0	0	7	21	58	9	5	2	95	102
Jun	0	12	91	0	103	23	22	4	0	4	53	156	1	6	1	1	9	22	38	0	0	0	60	69
Jul	0	2	2	1	5	5	8	2	0	1	16	21	2	7	0	0	9	2	11	3	1	1	18	27
Aug	20	21	35	0	76	51	68	23	0	7	149	225	0	4	6	0	10	26	49	4	0	3	82	92
Sep	4	4	2	0	10	10	14	3	0	2	29	39	8	18	7	1	34	11	17	6	0	0	34	68
Oct	3	10	21	0	34	57	64	104	12	9	246	280	12	17	5	0	34	6	3	1	0	0	10	44
Nov	2	23	15	0	40	2	1	8	0	0	11	51	1	2	0	0	3	1	3	0	0	0	4	7
Dec	28	51	32	0	111	48	348	35	0	0	431	542	2	47	15	0	64	4	100	14	0	4	122	186
Total	228	385	233	2	848	891	1019	304	12	49	2275	3123	61	188	74	2	325	439	806	209	6	12	1472	1797
	Mysis mixta												*Mysis stenolepis*											
Jan	0	3	0	0	3	20	22	0	7	5	54	57	0	0	0	0	0	12	10	0	7	1	30	30
Feb	0	0	0	0	0	0	4	0	0	1	5	5	0	0	0	0	0	1	0	0	0	0	1	1
Mar	0	1	0	0	1	8	134	0	0	48	190	191	0	1	0	0	1	0	8	0	0	7	15	16
Apr	0	0	0	0	0	0	29	2	0	3	34	34	0	0	0	0	0	1	11	0	0	5	17	17
May	0	19	5	0	24	0	63	38	0	0	101	125	0	0	0	0	0	0	2	0	0	0	2	2
Jun	0	22	13	0	35	0	52	65	0	0	117	152	0	1	0	0	1	0	0	0	0	0	0	1
Jul	0	7	0	0	7	0	149	110	0	0	259	266	0	0	0	0	0	0	14	0	0	0	14	14
Aug	0	18	0	0	18	4	136	0	0	0	140	158	0	0	0	0	0	0	26	0	0	0	26	26
Sep	0	9	0	0	9	0	16	0	0	0	16	25	0	0	0	0	0	0	10	0	0	0	10	10
Oct	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	20	0	0	0	20	20
Nov	0	0	0	0	0	5	4	0	0	0	9	9	0	0	0	0	0	5	9	0	0	0	14	14
Dec	2	5	0	0	7	18	17	0	1	0	36	43	0	0	0	0	0	1	1	0	0	0	2	2
Total	2	84	18	0	104	55	626	215	8	57	961	1065	0	2	0	0	2	20	111	0	7	13	151	153

M = male; F = female; Imm = immature; Ovig = ovigerous; Lar = larvigerous.
No ovigerous individuals were collected by the grab method.

occurred at 20–29 m. Peak density of immature stages occurred at 10–19 m and peak relative abundance of immature, ovigerous, and larvigerous stages was at 0.19 m (Table II). The frequency and relative abundance of *N. americana* (dredge) decreased significantly ($\alpha = 0.01$) with depth ($R = -0.56$, $R = -0.35$) as did the frequency in grab samples ($R = -0.29$, $\alpha = 0.05$).

Maximum numbers of *E. erythropthalma* were collected in intermediate depths in Cape Cod Bay (Table II). There was a marked increase in numbers at depths

TABLE II

Relationship to bathymetry (m) of common mysids by sex and stage in Cape Cod Bay.

Species Bathymetric Range (m)	Grab (No./m²)					Dredge (No./haul)						Grand total
	M	F	Imm	Lar	Total	M	F	Imm	Ovig	Lar	Total	
N. americana												
0–9	30	41	53	1	125	121	166	58	1	11	357	482
10–19	17	60	127	1	205	127	265	136	11	34	573	778
20–29	37	103	25	0	165	445	507	96	0	4	1052	1217
30–39	142	176	27	0	345	186	66	11	0	0	263	608
40–49	2	5	1	0	8	11	15	3	0	0	29	37
50–59	0	0	0	0	0	1	0	0	0	0	1	1
Total	228	385	233	2	848	891	1019	304	12	49	2275	3123
E. erythropthalma												
0–9	0	2	0	0	2	1	0	0	0	0	1	3
10–19	2	6	1	0	9	10	43	2	4	2	61	70
20–29	30	59	21	1	111	162	240	88	0	0	490	601
30–39	7	48	14	1	70	211	354	91	1	9	666	736
40–49	17	58	37	0	112	45	134	18	0	0	197	309
50–59	5	15	1	0	21	10	35	10	1	1	57	78
Total	61	188	74	2	325	439	806	209	6	12	1472	1797
M. mixta												
0–9	0	0	0	0	0	0	2	1	0	0	3	3
10–19	0	13	14	0	27	0	47	6	0	8	61	88
20–29	0	15	1	0	16	16	98	7	2	14	137	153
30–39	0	25	2	0	27	12	342	142	0	4	500	527
40–49	2	27	1	0	30	16	105	59	3	31	214	244
50–59	0	4	0	0	4	11	32	0	3	0	46	50
Total	2	84	18	0	104	55	626	215	8	57	961	1065
M. stenolepis												
0–9	0	0	0	0	0	3	19	0	0	1	23	23
10–19	0	2	0	0	2	5	53	0	0	5	63	65
20–29	0	0	0	0	0	9	31	0	4	5	49	49
30–39	0	0	0	0	0	1	6	0	1	1	9	9
40–49	0	0	0	0	0	2	2	0	2	1	7	7
50–59	0	0	0	0	0	0	0	0	0	0	0	0
Total	0	2	0	0	2	20	111	0	7	13	151	153

M = male; F = female; Imm = immature; Ovig = ovigerous; Lar = larvigerous.
No ovigerous individuals were collected by the grab method.

greater than 20 m. The highest density occurred between 20 and 29 m. Immature forms reflected the same density distribution patterns as adults. Ovigerous and larvigerous stages (dredge) were collected from 10 to 59 m with a peak for the latter in the 30–39 m range. The frequency (grab) of this species increased significantly ($\alpha = 0.01$) with depth (R = 0.48).

Maximum numbers of *M. mixta* were found at middle depths (Table II). Density of immature stages was highest at 30–39 m. Ovigerous and larvigerous stages also tended to occupy middle depths (Table II). The frequency of *M. mixta* in grab (R = 0.28) and dredge (R = 0.27) samples increased significantly ($\alpha = 0.05$) with depth.

The depth range of *Mysis stenolepis* resembled that of *N. americana* more than that of the other two common mysids (Table II). The highest relative abundance occurred at 10–19 m and declined rapidly at depths greater than 30 m. Larvigerous stages occurred from 0 to 49 m and ovigerous stages occurred from 20 to 49 m. Frequency and relative abundance decreased (R = −0.33, R = −0.28) significantly ($\alpha = 0.05$) with depth.

Relationship to bottom water temperature

Most *N. americana* were caught in bottom waters at temperatures between −1.5 and 8.1°C (Table III). Numbers declined above 8.1°C. Density of immature stages was highest between 6.0 and 8.1°C and relative abundance of immature stages was highest at 8.2 to 12.0°C. Ovigerous stages were collected at 8.2 to 12.0°C, and larvigerous stages (dredge) were sampled at temperatures of 3.3 to 23.5°C. The density and relative abundance of *N. americana* decreased (R = −0.47, R = −0.46) significantly ($\alpha = 0.01$) with increasing temperature.

Most *E. erythropthalma* occurred from −1.5 to 8.1°C (Table III) with a marked decline above 8.1°C. Immature, ovigerous, and larvigerous stages were found at the same temperature range as adults. Density (R = −0.65), relative abundance (R = −0.54), and frequency (grab R = −0.52, dredge R = −0.76) of *E. erythropthalma* decreased significantly ($\alpha = 0.01$) with increasing temperature.

Maximum densities of *M. mixta* occurred at temperatures of 3.3 to 8.1°C, whereas maximum relative abundance occurred from −1.5 to 8.1°C (Table III). Immature stages from both types of collecting gear were most abundant from 3.3 to 8.1°C. In contrast, ovigerous and larvigerous stages (dredge) were relatively more abundant between −1.5 and 5.9°C. The frequency of *M. mixta* in grab (R = −0.38) and dredge samples (R = −0.67) decreased significantly ($\alpha = 0.05$, $\alpha = 0.01$) with increasing temperature.

Relative abundance of *M. stenolepis* was generally high throughout a range of −1.5 to 23.5°C (Table III). This was the most eurythermal species of the common Cape Cod Bay mysids. Immature stages were more abundant in warmer temperatures (6.0–23.5°C), whereas ovigerous and larvigerous stages were more abundant below 6.0°C. The frequency and relative abundance of *M. stenolepis* decreased with increasing temperature, but the relationships were not statistically significant.

Relationship to sediment type

Maximum density of *N. americana* occurred in clayey-silt with relatively high numbers in sand and silt (Table IV). This species was also collected infrequently in gravel. Maximum relative abundance occurred in sand, followed in decreasing order by clayey-silt and silt, and gravel. Ovigerous and larvigerous stages were only collected in sand. The frequency (dredge) of *N. americana* decreased with increasing

TABLE III

Bottom water temperature distribution of common mysids by sex and stage in Cape Cod Bay.

Species Temperature Range (°C)	Grab (No./m^2)					Dredge (No./haul)						Grand total
	M	F	Imm	Lar	Total	M	F	Imm	Ovig	Lar	Total	
N. americana												
−1.5–3.2	130	137	29	0	296	234	281	58	0	0	573	869
3.3–5.9	40	122	8	0	170	439	198	70	0	4	711	881
6.0–8.1	35	71	131	1	238	108	381	43	0	26	558	796
8.2–12.0	2	25	19	0	46	56	66	104	12	8	246	292
12.1–23.5	21	30	46	1	98	54	93	29	0	11	187	285
Total	228	385	233	2	848	891	1019	304	12	49	2275	3123
E. erythropthalma												
−1.5–3.2	29	51	30	0	110	264	451	147	0	2	864	974
3.3–5.9	16	69	20	1	106	123	184	45	2	1	355	461
6.0–8.1	4	50	21	1	76	49	166	16	4	9	244	320
8.2–12.0	12	16	2	0	30	3	5	1	0	0	9	39
12.1–23.5	0	2	1	0	3	0	0	0	0	0	0	3
Total	61	188	74	2	325	439	806	209	6	12	1472	1797
M. mixta												
−1.5–3.2	0	4	0	0	4	21	143	0	5	48	217	221
3.3–5.9	2	47	4	0	53	14	177	98	2	9	300	353
6.0–8.1	0	33	14	0	47	15	300	116	1	0	432	479
8.2–12.0	0	0	0	0	0	5	6	1	0	0	12	12
12.1–23.5	0	0	0	0	0	0	0	0	0	0	0	0
Total	2	84	18	0	104	55	626	215	8	57	961	1065
M. stenolepis												
−1.5–3.2	0	1	0	0	1	14	14	0	7	4	39	40
3.3–5.9	0	0	0	0	0	1	15	0	0	9	25	25
6.0–8.1	0	1	0	0	1	4	34	0	0	0	38	39
8.2–12.0	0	0	0	0	0	1	20	0	0	0	21	21
12.1–23.5	0	0	0	0	0	0	28	0	0	0	28	28
Total	0	2	0	0	2	20	111	0	7	13	151	153

M = male; F = female; Imm = immature; Ovig = ovigerous; Lar = larvigerous.
No ovigerous individuals were collected by the grab method.

median sediment size (ϕ) (R = −0.64, α = 0.01), increased with percent sand (R = 0.53, α = 0.01), and decreased with percent clayey-silt (R = −0.51, α = 0.01). Relative abundance also declined with percent silt (R = −0.37) and the frequency (grab) decreased with percent clayey-silt (R = −0.57, α = 0.01).

Maximum density of *E. erythropthalma* was in clayey-silt and silt, with immature stages most abundant in clayey-silt (Table IV). Maximum relative abundance occurred in silt, clayey-silt, and sand. Ovigerous and larvigerous stages were collected throughout a range of sand to clayey-silt. The frequency of *E. erythropthalma* in grab (R = 0.78) and dredge (R = 0.72) samples, density (R = 0.59), and relative abundance (R = 0.66) increased significantly (α = 0.01) with decreasing ϕ. The fre-

TABLE IV

Sediment distribution of common mysids by sex and stage in Cape Cod Bay.

Species Sediment Type	Grab (No./m^2)					Dredge (No./haul)						Grand total
	M	F	Imm	Lar	Total	M	F	Imm	Ovig	Lar	Total	
N. americana												
gravel	0	7	1	0	8	12	11	9	0	0	32	40
sand	46	99	181	2	328	527	426	215	12	49	1229	1557
silt	16	63	22	0	101	208	516	66	0	0	790	891
clayey-silt	166	216	29	0	411	144	66	14	0	0	224	635
Total	228	385	233	2	848	891	1019	304	12	49	2275	3123
E. erythropthalma												
gravel	0	0	0	0	0	0	0	0	0	0	0	0
sand	2	8	1	0	11	82	106	21	4	2	215	226
silt	20	68	23	0	111	240	437	133	1	5	816	927
clayey-silt	39	112	50	2	203	117	263	55	1	5	441	644
Total	61	188	74	2	325	439	806	209	6	12	1472	1797
M. mixta												
gravel	0	5	2	0	7	0	0	0	0	0	0	7
sand	0	18	12	0	30	0	74	15	0	11	100	130
silt	0	28	4	0	32	48	378	200	5	32	663	695
clayey-silt	2	33	0	0	35	7	174	0	3	14	198	233
Total	2	84	18	0	104	55	626	215	8	57	961	1065
M. stenolepis												
gravel	0	0	0	0	0	0	0	0	0	0	0	0
sand	0	1	0	0	1	9	87	0	0	10	106	107
silt	0	1	0	0	1	8	11	0	5	3	27	28
clayey-silt	0	0	0	0	0	3	13	0	2	0	18	18
Total	0	2	0	0	2	20	111	0	7	13	151	153

M = male; F = female; Imm = immature; Ovig = ovigerous; Lar = larvigerous.
No ovigerous individuals were collected by the grab method.

quency and density increased significantly ($\alpha = 0.01$) with percent silt (R = 0.70, R = 0.52) and percent clayey-silt (R = 0.67, R = 0.58), while relative abundance increased significantly ($\alpha = 0.05$) with percent silt (R = 0.34). In contrast, the frequency of *E. erythropthalma* in grab (R = −0.50) and dredge (R = −0.53) samples, density (R = −0.50), and relative abundance (R = −0.36) decreased significantly ($\alpha = 0.01$, $\alpha = 0.01$, $\alpha = 0.01$, $\alpha = 0.05$) with percent sand.

Mysis mixta occurred at greatest density in sand through clayey-silt (Table IV), with immature stages primarily in sand. Maximum relative abundance occurred in silt followed by clayey-silt and sand. Larvigerous and ovigerous stages were found throughout a sand to clayey-silt range. The frequency of *M. mixta* (dredge) increased significantly with increasing ϕ (R = 0.68, $\alpha = 0.01$), percent silt (R = 0.34, $\alpha = 0.05$), and percent clayey-silt (R = 0.44, $\alpha = 0.05$) and decreased with percent sand (R = −0.51, $\alpha = 0.01$). The frequency of this species (grab) decreased significantly ($\alpha = 0.05$) with percent sand (R = −0.28) and increased with percent silt (R = 0.32) and percent clayey-silt (R = 0.45, $\alpha = 0.01$). The density decreased significantly ($\alpha = 0.01$) with percent sand (R = −0.46).

Most *M. stenolepis* were caught in sand (Table IV). Larvigerous stages were relatively more abundant in sand, but ovigerous stages were collected in silt and clayey-silt. The relative abundance of *M. stenolepis* significantly increased ($\alpha = 0.05$) with percent sand (R = 0.33) and decreased with percent silt (R = −0.42).

Discussion

Collecting gear

The grab sample data presented here provide some of the first quantitative estimates of densities of life history stages of mysids in relation to seasonal and environmental factors for the northeast United States. However, there is some collecting bias between the grab and dredges. Dredge hauls frequently collected more life history stages, particularly ovigerous and larvigerous forms, than grab samples (Table I). Moreover, grab samples underestimated the frequency and numbers of *M. stenolepis* (Table I). Accordingly one's perception of mysid distribution patterns can be significantly affected by type of collecting gear used (Mauchline, 1980).

Geographic distribution

Erythrops erythropthalma and *M. mixta* are considered amphi-Atlantic species. In contrast, *M. stenolepis* and *N. americana* are considered warm temperate to tropical water species (Wigley and Burns, 1971). Mauchline (1980) stated that species living south of 60°N, including *E. erythropthalma* and *M. mixta*, may intrude into the Arctic Ocean regularly or sporadically. According to him *M. stenolepis* and *N. americana* belonged to a fauna confined to the western Atlantic between 60°N and 40°N. *Mysis mixta* was also considered amphi-Atlantic by Mauchline (1980) but also characteristic of coastal areas. Occurrence in New England waters is well documented for species collected in this study (Fish, 1925; Whiteley, 1948; Wigley, 1964).

Seasonal distribution

Wigley and Burns (1971) found ovigerous and larval stages of *N. americana* from March to October with the largest numbers in March through June and August through October along the northeastern U. S. continental shelf and slope. Immature stages were particularly numerous in August and December. The situation in Cape Cod Bay differed in that large pulses of adults occurred in February, April, and December, ovigerous stages occurred only in October, and larval stages occurred from April to October with a May peak (Table I). Hopkins (1965) reported three major spawning peaks of *N. americana* (April–May, June, August) in Delaware Bay. He encountered a few ovigerous stages as late as January and February. Williams (1972) reported the greatest abundance of *N. americana* from November to May or June in North Carolina estuaries. He showed that ovigerous or larvigerous stages occurred in every month but November.

Mauchline (1980) proposed several major types of mysid reproduction and succession of generations. His classification included species with 0.5, <1, 1, 2, 3, and ≥3 generations per year. *Neomysis americana* may not fit easily into Mauchline's (1980) classification scheme. There is evidence to indicate that *N. americana* produces two generations a year on Georges Bank (Wigley and Burns, 1971) and in Cape Cod Bay (Table I), three in Delaware shallow waters (Hopkins, 1965), and perhaps three or more generations in North Carolina estuaries (Williams, 1972). If this pattern is accurate, it suggests a latitudinal shift of reproduction for *N. americana*.

According to Wigley and Burns (1971), ovigerous stages of *E. erythropthalma* occurred only in August and larvigerous stages in August and September along the Atlantic coast. This contrasts with our findings in Cape Cod Bay of ovigerous stages in May and July and larvigerous stages in January, May–September, and December (Table I). These findings tend to confirm the tentative conclusion of a lengthy spawning period proposed by Wigley and Burns (1971). *Erythrops erythropthalma* probably produces two generations per year and falls within Mauchline's (1980) classification.

Wigley and Burns (1971) concluded that *M. mixta* had two definite age groups in both spring and fall. Immature stages were common in May and October. No ovigerous specimens were present in their collections. The only indication of spawning season was the presence of small (5.3–6.3 mm) individuals in May, suggesting a late winter or early spring spawning. Within Cape Cod Bay, adult, peaks occurred in later winter and summer with a July peak for immature stages (Table I). Tattersall (1951) recorded many occurrences of adults in August and September but made no references to larvigerous and ovigerous stages. Records of ovigerous stages in January and larvigerous stages in January through April (March peak) (Table I) confirm the late winter/early spring spawning period proposed by Wigley and Burns (1971). The grossly unbalanced sex ratio reported for *M. mixta* from broad ranging samples on the continental shelf was also recorded in the more restricted confines of Cape Cod Bay. Different habitat preferences for males and females, different environmental conditions for reproduction and larval development, or short-lived life cycle for males may explain this pattern.

Although data for *M. stenolepis* are sparse, there is a suggestion of peaks for adults in winter (January) and summer (August) and for larvigerous stages in late winter/early spring (Table I). Ovigerous stages were collected only in January. This view agrees with earlier versions provided by Smith (1879) and Tattersall (1951). According to Mauchline's scheme, *M. stenolepis* and probably *M. mixta* would belong to species producing one generation per year.

Relation to bathymetry

Mauchline (1980) proposed a bathymetric classification of mysids that included recognition of the ecological significance of salinity (freshwater and brackish). Exclusive of brackish and freshwater species, he recognized a spectrum ranging from littoral, to shallow shelf, to eurybenthic shelf, to bathypelagic.

Wigley and Burns (1971) established five depth categories from which mysids were most frequently caught. *Neomysis americana*, E. erythropthalma, and *M. mixta* were listed as eurybathic shelf species (range 1–421 m), and *M. stenolepis* was cited as a shore species (intertidal). Within Cape Cod Bay there was evidence of spatial partitioning in terms of bathymetric stratum. *Neomysis americana* and *M. stenolepis* were characteristic of shallow and intermediate depths, while *E. erythropthalma* and *M. mixta* were characteristic of intermediate to greater depths (Table II). The associations of *N. americana* and *M. stenolepis* with shallow water and of *E. erythropthalma* with deeper water were reported previously (Segerstrale, 1945; Tattersall, 1951, 1954; Bousfield, 1956; Wigley, 1964; Wigley and Burns, 1971). In contrast, Hulburt (1957) found more *N. americana* at greater depths in Delaware Bay. Their low abundance in shallow water may have been due in part to the presence of caridean shrimp (*Crangon septemspinosa* (Say), *Palaemontes vulgaris* (Say), *P. pugio* (Holthuis)) which are very abundant in shallow waters of Delaware Bay (Price, 1962).

The segregation of Cape Cod Bay species pairs by depth is indicative of zonation, which reduces competition for space. Zonation of nearshore mysids (0–17 m) was described from a sand bottom on the open coast of California (Clutter, 1967). He concluded that zonation probably developed in response to the availability of food imposed by nearshore circulation. This relationship cannot be ignored in Cape Cod Bay; a case for multivariate environmental interaction is discussed later. In terms of Mauchline's (1980) bathymetric classification *N. americana* and *M. stenolepis* in Cape Cod Bay would fall within the littoral to shallow shelf habitat and *E. erythropthalma* and *M. mixta* would fit the shallow shelf to eurybenthic shelf habitat.

Relationship to bottom water temperature

Neomysis americana is considered to be eurythermic, found at bottom water temperatures from 0 to 25°C (Wigley and Burns, 1971). Within Cape Cod Bay *N. americana* occurred throughout a similar temperature range, but their maximum distribution was between −1.5 and 8.1°C (Table III). Specimens from Delaware Bay were most abundant at lower temperatures (Hulburt, 1957). *Erythrops erythropthalma* showed a bottom water temperature distribution similar to that of *N. americana*, but its abundance peaked in even lower temperatures (−1.5 to 3.2°C) (Table III). *Mysis stenolepis* occurred throughout the local temperature range, but *M. mixta* was only collected below 12.0°C (Table III). The peak of the latter species was 6.0–8.1°C. The former species, together with *N. americana*, occurred in appreciable numbers above 12.0°C. The local temperature occurrence of the two species of *Mysis* was consistent with their shallow and deeper water habits.

Bottom water temperature changes seasonally. However, there was evidence for interaction between temperatures and depth on abundance and frequency of mysids. Maximum abundance of *N. americana*, *E. erythropthalma*, and *M. stenolepis* occurred in a temperature range of −1.5 to 8.1°C, which coincided with high seasonal numbers recorded for January through March. A similar relationship can be seen for *M. mixta* with maximum abundance in 6.0–8.1°C which coincided with high seasonal numbers recorded for May and July. Seasonal effects are evident in these relationships.

However, the relationship between bottom water temperature and the deeper water mysid pair (*E. erythropthalma* and *M. mixta*) was further complicated by depth-temperature interaction. A marked summer thermocline was reported in Cape Cod Bay from mid-April until Mid-October (Young *et al.*, 1971). The annual temperature at 20 to 26 m ranged from −1.5 to 10°C. The lowest extent of the thermocline defined by the 5°C isotherm intersected the sea floor at approximately 26 m. Even though mysid distribution is influenced by seasonal effects of bottom water temperature, the latter is influenced by bathymetry. It might be expected that the shallow water pair of mysids are more responsive to seasonal water temperatures, whereas the deeper water pair are more affected by depth-bottom temperature relationships. Emberton (1981) showed that selected taxa of subtidal meiofauna in Cape Cod Bay were significantly influenced by season-depth interactions. Season was more important in shallow water, whereas there was a time lag at greater depths in terms of meiofauna density.

Relationship to sediment type

Mauchline (1980) cited many cases of sediment preference for hyperbenthic mysids. Wigley and Burns (1971) summarized the sediment distribution of mysids as follows: *N. americana* and *E. erythropthalma* on sand, *M. stenolepis* on sand and *Zostera*, and *M. mixta* on a variety of sediments. However, the present study showed that silt and clayey-silt played an important role in the distribution of Cape Cod Bay mysids (Table IV). Williams (1972) cited evidence that *N. americana* in North Carolina estuaries commonly occurred over sediments of clay and silt-sized particles. Young and Rhoads (1971) collected quantitative samples in Cape Cod Bay and reported *N. americana* from sand and clayey-silt.

In this study, *N. americana* had a wide sediment range occurring in gravel through clayey-silt (Table IV). Even though maximum abundance (dredge) was reported in sand, relatively high numbers were also recorded in silt and clayey-silt. Moreover, maximum density was recorded from clayey-silt. This broad sediment range, together with its eurythermic characterization and broad salinity range (Hulburt, 1957), is consistent with its occupancy of coastal areas and estuaries which normally display rapidly changing environmental conditions. The detrital load of estuaries and the feeding habit of *N. americana* are also involved in this association.

In view of the bias toward sand samples in the collection, maximum abundance and occurrence of *E. erythropthalma* in silt and clayey-silt indicates the importance of this sediment type. This relationship is supported by other findings (Young and Rhoads, 1971). Thus, the earlier view of the sediment distribution of *E. erythropthalma* as characteristically occurring in sand (Wigley and Burns, 1971) should be amended to include bottoms with significant amount of silt and clayey silt.

Mysis mixta had a broad sediment range comparable to *N. americana* but occurred most abundantly in Cape Cod Bay in silt and clayey-silt (Table IV). This distribution is generally consistent with an earlier view (Wigley and Burns, 1971). *Mysis stenolepis* peaked in sand in Cape Cod Bay, but this species may live in sediment containing as high as 18% silt or 12% clayey-silt. It appears that fine grain sediment can be considerably more important in the ecology of these four mysids than previously recognized. The relationships among fine sediment, particulate organics, microbiota, and mysid feeding habits deserve attention (Mauchline, 1980) because *M. stenolepis* may be able to digest cellulose (Wainwright and Mann, 1982).

There was evidence of significant relationships between mysid frequency, density, and relative abundance and sediment type. Sediment decreases in modal size and increases in total clay and carbon contents with depth in Cape Cod Bay, and seston flux is 10 times greater at the deeper muddy stations than at the shallow sandy stations (Young *et al.*, 1971). Young *et al.* reported difficulty in determining which environmental factor was most important in separating zones of polychaetes in Cape Cod Bay because the isopleths of 10°C, 15–20 m, and 20% mud closely coincided. Their findings are consistent with the view of interactions among bottom water temperatures, depth, and sediment distribution. Accordingly, distributions of mysid species are probably influenced by these interactions. Since the same interactions are not as well defined along the northeastern part of the bay, seasonal-temperature factors may be more important here.

In summary, zonation of these mysids was related to depth-temperature-sediment interactions within a seasonal framework. These multifactorial environmental effects were expressed by a shallow water, silt-sand to sand pair of mysids (*N. americana* and *M. stenolepis*) and a deeper water, silt to clayey-silt pair (*E. erythropthalma* and *M. mixta*). Evidence for partitioning related to biotic factors was not included in this study, but evidence of considerable predation on mysids by finfish and competition through co-occurrences of mysids has been presented elsewhere (Wigley and Burns, 1971; Mauchline, 1980). In general, these mysids fall within Mauchline's (1980) bathymetric and reproductive classifications, with differences from these distributions associated with regional and seasonal conditions.

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